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How good is the fossil record of arthropods? An assessment using the stratigraphic congruence of cladograms

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A total of 179 published cladograms of arthropods was tested for their congruence with the palaeontological record. Congruence for data sets including 510 tetrapod and 157 fish trees was also calculated for comparison. Results provide support for the hypothesis that the fossil record of arthropods is less complete (at levels of stratigraphic and taxonomic resolution pertinent to most macroevolutionary studies) than the records of several other taxa. Differences in tree size, shape, balance and the distribution of first stratigraphic appearances (potential sources of bias) were controlled for by various randomization procedures. Most measures of congruence for arthropods were statistically poorer than those for other groups, even when the sample was divided into broad temporal bins. Many of the most robust and widely reproduced sister groupings of arthropods are attended by ghost ranges of many tens or hundreds of millions of years. Fossils of a number of presently very diverse and abundant arthropod groups are conspicuously absent from the record, despite many spectacular examples of the detailed preservation of others. There is probably no single reason for the apparently poor record of arthropods. Low preservation potential, small size of individuals, small numbers of individuals, and restricted palaeobiogeography almost certainly play a role in particular cases.
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1. INTRODUCTION

Modern arthropods are enormously abundant and diverse, having exploited virtually every possible habitat, mode of life and developmental strategy. Some 78% of described extant species are arthropods, 90% of which are insects (Brusca and Brusca 1990). Some of the earliest, most conspicuous and informative metazoan fossils are also arthropods, and the phylum has been a major constituent of the biosphere throughout the history of the Phanerozoic (Sepkoski *et al.* 1981; Sepkoski and Labandeira 1993). The arthropod exoskeleton is principally composed of chitin and protein, and its thickness is highly variable depending on biomechanical requirements. Even the thickest cuticle is unlikely to be preserved as a fossil in all but the most exceptional circumstances. Some arthropods, notably trilobites, eumalacostracans and ostracods, have also reinforced parts of their skeletons with calcium carbonate, a much more resilient material.

Despite a low preservation potential, non-mineralized arthropods within conservation Lagerstätten (sites of exceptional preservation: Seilacher 1990) are amongst the most exquisitely detailed fossils known. Numerous modes of diagenesis contribute to a record that includes the enigmatic forms of the Cambrian Burgess Shale (Briggs *et al.* 1994; preserved in thin organic films (Butterfield 1990) and clay minerals (Orr *et al.* 1999) that require painstaking dissection), the three-dimensional phosphatized crustaceans and other groups from the Cambrian Orsten (yielding three-dimensional detail under the scanning electron microscope; Müller 1983; Walossek and Müller 1992), and the pyritized Devonian material of the Hunsrück Slate in Germany (requiring

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X-ray photography to reveal its intricate detail; Størmer 1968; Bartels *et al.* 1998; Haas 1999). Many small- to medium-sized terrestrial arthropods are also beautifully preserved in amber (Poinar 1992) or rarely permineralized in silica (e.g. the Rhynie Chert; Whalley and Jarzembowski 1981).

Notwithstanding examples of excellent preservation, there are many conspicuous gaps in the arthropod record. Patchy records within groups (e.g. Fara and Benton 2000) are not the primary concern here. Rather, the discussion focuses on the gaps between the first occurrences of sister groups. If the fossil record were complete at a given level of resolution (e.g. stages), then sister taxa would be expected to appear as fossils at the same time (e.g. in the same stage). However, the fossil record is not complete, and the first occurrences of sister taxa are often widely separated. In such cases, a ghost range is hypothesized between the two points of origin (Benton 1995).

Results from a statistical treatment of the extent of ghost ranges in the fossil record of arthropods and other groups (based on a large sample of 1000 published cladograms) are presented. Inferences about the sequence of phyletic branching (cladograms derived from distributions of morphological or molecular character states, plus knowledge of character polarity) provide models concerning the history of a given group. The order in which taxa appear as fossil through geological time offers an independent source of data on the same history. The extent to which branching order and the order of fossil occurrences concur (their congruence) may have implications for the accuracy of phylogenetic reconstruction (in the case of particular trees), or for the completeness of the fossil record, or both. Unless there are compelling reasons to suppose that phylogeny is intrinsically more difficult to reconstruct for one group than another (or that there are other sources of bias), differences in congruence for large samples of trees may reflect differences in the completeness of the fossil record.

2. METHODS

2.1. The data base

A data set of arthropod cladograms was compiled from a trawl of the last 15 years of biological and palaeontological journals including *Lethaia, Palaeontology, Paleobiology, Systematic Biology* and *Systematic Entomology*, plus general invertebrate texts and several large multi-author volumes. While this is not a comprehensive inventory of published trees from a given period, it does offer a relatively unbiased sample. A full list of the sources for all 179 cladograms is given at the University of Bristol website (2001a). Results for several of these trees are discussed in detail, and summary statistics are presented for the entire sample. The arthropod data were compiled in conjunction with information on other groups (Benton *et al.* 2000). The combined data set included 34 cladograms of plants, 34 of basal deuterostomes and calcichordates, 60 of echinoderms, 26 of invertebrates (other than arthropods, basal deuterostomes, calcichordates and echinoderms), 157 of fish, and 510 of tetrapods (including 30 of basal tetrapods, 211 of amniotes, reptiles and birds, and 269 of mammals). For comparison, results from the arthropod data are presented alongside selected results from fish, tetrapods, and all taxa taken together (1000 cladograms in total).

The primary source of stratigraphic range information was Benton (1993) and references therein. In some cases, more recent data were available within the papers containing the trees themselves. Originations and extinctions for terminal taxa were coded according to the stratigraphic scheme of Harland (1990), and to the level of series and stages. The Phanerozoic was divided into 79 time intervals, with an average duration of approximately 7.25 million years. A further two divisions were recognized into the Proterozoic (Sinian and Riphean). A list of stratigraphic divisions and ages is distributed as part of the 'Ghosts' program for calculating stratigraphic congruence, available from the University of Bristol website (2001b).

2.2. Congruence indices

Methods for assessing the congruence between phylogeny and stratigraphy have been discussed in detail elsewhere (e.g. Norrell and Novacek 1992; Huelsenbeck 1994; Siddall 1996; Benton and Hitchin 1996; Wills 1999; Benton *et al.* 2000; Wagner 2000a). Three basic indices are considered here. The relative completeness index (RCI) and

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gap excess ratio (GER) make reference to the extent of ghost ranges between pairs of sister terminals, sister clades or pairs of terminals and clades. Where one member of each pair originates before the other, a ghost range is inferred between the two dates of origin. The sum of ghost ranges over the entire tree is referred to as the minimum implied gap (MIG). A given distribution of origination dates imply a *minimum* possible MIG (G_{min}) regardless of the tree on which they are distributed. This is equivalent to the difference between the oldest origin and the youngest origin. There is also a maximum possible MIG (or G_{max}), equivalent to the sum of the differences between the oldest origin and all other origins. The MIG for the observed tree and distribution of stratigraphic range data must lie somewhere between G_{min} and G_{max}, and the GER (Wills 1999) expresses whether MIG is closer to G_{max} (GER = 0) or G_{min} (GER = 1). Formally: $GER = 1 - (MIG - G_{min})/(G_{max} - G_{min})$. The GER provides an index of stratigraphic congruence, based on the extent of ghost ranges.

The RCI of Benton (1995) takes account not only of the MIG (the extent of ghost ranges) but also of the extent of observed ranges, SRL (standard range length). The SRL is given by the sum of the differences between the first and last observed occurrences of each terminal taxon as fossils. This is independent of any tree topology. Formally: $RCI = 1 - (MIG/SRL) \times 100\%$. The RCI is scaled from 100% (where all taxa originate at the same time) to minus infinity, and is an index of the extent of observed fossil ranges as well as the congruence between phylogeny and stratigraphy.

The stratigraphic consistency index (SCI) of Huelsenbeck (1994) makes no reference to ghost ranges, but rather considers the congruence of each internal node of the cladogram. Nodes are dated according to the time of origin of the oldest terminal they support. A node is congruent if its sister node or sister terminal is as old or older than it is. The SCI is then given as the number of congruent nodes over the total number of nodes. Like the GER, the SCI is solely an index of congruence, rather than congruence and the extent of observed ranges (as in the case of the RCI).

It has been demonstrated (Siddall 1996, 1998; Wills 1999) that SCI, RCI and GER values are influenced by a variety of factors that preclude straightforward comparison between trees of different sizes and balance, and comprising taxa that originate with different frequencies through the stratigraphic column. Many of these factors can be controlled using a form of randomization test (Huelsenbeck 1994; Wills 1999). Tree topology is held constant, and the stratigraphic ranges are reassigned over the tree a large number of times (e.g. 1000). For each randomized reassignment, the GER and SCI are recalculated. The GER and SCI 'significances' are given by the percentage of randomized range reassignments that yield values of congruence better than or equal to those from the original data. RCI significance will be equivalent to GER significance (the SRL, G_{min} and G_{max} are all invariant for a given set of range data, and only the MIG varies in either case). The randomization procedure probably does not constitute a *test* of significance in the strict sense, since optimal congruence is not necessarily the expectation from real data. Wills (1999) proposed the use of the GER and SCI significances (rather than raw values) as the basis for comparing congruence between cladograms of different sizes, and with different topologies. Differences in the times of first occurrences also bias the range and distribution of SCI values it is possible to obtain.

An alternative permutation procedure was applied to a small number of cladograms. This compared the congruence of the original tree with that of 1000 random *trees*. Since the tree is randomized, so are the assignments of ranges. Biases in congruence related to tree topology are therefore *not* controlled for. Greater differences between the range-permuted and tree-permuted significances would be anticipated for the SCI than the GER, as the latter is less influenced by topology. Finally, the randomized trees were themselves subjected to 1000 randomized range reassignments. This attempted to test whether the original tree was significantly more congruent than the random phylogenies, with a secondary control for topological bias (results should therefore be broadly similar to those from range reassignments over the original topology).

3. CONSPICUOUS GAPS IN THE ARTHROPOD FOSSIL RECORD

3.1. Gaps between the major arthropod groups

While there are several competing phylogenies for most arthropod groups, many sister-group relationships appear in most if not all phylogenies and may have implications for ghost ranges extending through hundreds of millions

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of years. Enormous controversy has surrounded the relationships of the major groups (Edgecombe 1998; Fortey and Thomas 1998).

The first trilobite fossils are undoubtedly Lower Cambrian in age (Romano *et al.* 1993). The appearance of several faunal provinces of trilobites already differentiated in the Atdabanian record has prompted speculation that the group diversified some time in the Precambrian (Fortey *et al.* 1996, 1997). Many workers (e.g. Paulus 1979; Weygoldt 1979; Emerson and Schram 1998; Wills *et al.* 1994, 1995) have considered the chelicerates to be the sister group of the trilobites, but the age and identity of the earliest chelicerate is controversial. The Lower Cambrian *Eolimulus* is known only from carapaces, and cannot be assigned to the group with confidence (Bergström 1968). Claims that the Middle Cambrian *Sanctacaris* is a chelicerate (based primarily on its pattern of tagmosis; Briggs and Collins 1988) have not been supported in cladistic analyses (e.g. Wills *et al.* 1995). Likewise, although there are compelling similarities between the Middle Cambrian *Sidneyia* and xiphosurans (particularly in details of appendage morphology; Bruton 1981), *Sidneyia* has never (to the best of my knowledge) been resolved as a chelicerate or an immediate relative in analyses based on larger suites of characters. In this context, the interpretation of what constitutes the 'head' may be critical (Schram and Emerson 1991). The placement of the Lower Cambrian *Fuxianhuia* within the chelicerates (Wills 1996) is contentious, but this animal is certainly an arachnomorph rather than a basal euarthropod (Chen *et al.* 1995: Dunlop and Selden 1998). Chlupač and Havlúcek (1965) originally described *Kodymirus*, from the Cambrian of Bohemia, as an aglaspid, although redescription has prompted its reinterpretation as a eurypterid (Chlupač 1995). Five pairs of moderately well-differentiated cephalic limbs are known in this animal. However, the presence of a more anterior pair of appendages (chelicerae) can only be inferred. The affinities of the pycnogonids remain contentious (Wheeler *et al.* (1993) resolved them as the sister group to the chelicerates using a total evidence data set), but all pygnogonid fossils are Devonian. There is good evidence from molecules and morphology that pentastomids are crustaceans (and probably the sister group of the Branchiura; Grygier 1983; Spears and Abele 1998). Finally, a consensus is emerging that tardigrades are basal to the Arthropoda (Brusca and Brusca 1990; Nielsen 1995; Monge-Nájera 1995; Wills *et al.* 1995). The first undisputed chelicerates therefore date from the Arenigian (Selden 1993; Dunlop and Selden 1998). However, a number of arachnomorph genera (including, among others, *Sanctacaris* and *Sidneyia*) appear more closely related to chelicerates than any other *extant* group (Wills *et al.* 1995). These extend the known record of the clade that comprises chelicerates and most non-trilobite arachnomorphs down to the Lower Cambrian. Although this obviates any appreciable ghost range between trilobite and non-trilobite arachnomorphs, a ghost range of at least 43 million years exists between chelicerates *sensu stricto* and their nearest relatives (aglaspids according to Wills *et al.* (1995)).

The earliest crustacean fossils are almost certainly ostracods (Whatley *et al.* 1993) and phyllocarids (Briggs *et al.* 1993), dating from the Lower Cambrian (Schram 1982). By the Middle Cambrian, cirripede fossils are also recorded (Wills 1963), along with a range of genera of uncertain affinities (Walossek and Müller 1992; Wills 1998). The unity of the Atelocerata, the clade comprising the Hexapoda (or Insecta) and Myriapoda, is uncertain. Both Hexapoda and Myriapoda first appear as fossils early in the Devonian (Ross and Jarzembowski 1993; Ross and Briggs 1993). Cladograms that split the Atelocerata typically resolve the Hexapoda as the sister group of the Crustacea (e.g. Akam and Averof 1995; Boore *et al.* 1995) and the Myriapoda lower in the arthropod tree (e.g. Turbeville *et al.* 1991; Ballard *et al.* 1992) (implying two long ghost ranges from the Lower Cambrian to the Lower Devonian). Molecular data have also placed the myriapods opposing the chelicerates (Min *et al.* 1998; Weygoldt, 1998) (chelicerates can be taken to stand for all arachnomorphs), another difference of 159 million years. Cladograms that retain the Atelocerata as a natural group either resolve them opposite the Crustacea (Snodgrass 1938; Wheeler *et al.* 1993), or diverging basally from the rest of the euarthropods (Wills *et al.* 1995; Emerson and Schram 1998). A ghost range of 159 million years is implied in either case.

3.2. Gaps between the major groups of Crustacea

There have been relatively few attempts to infer the phylogeny of the entire Crustacea. Several smaller studies have been conducted on major constituent groups, such as the Eumalacostraca (and subgroups), Branchiopoda and

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Copepoda. Some relationships have arisen on many or most occasions, and several of these imply the existence of extensive ghost ranges.

Several taxa have been forwarded as the most primitive crustaceans, notably the Cephalocarida, Anostraca and Remipedia. None of these are among the oldest fossils for the group, and all must be joined to the rest of the clade via a ghost range of between 146 and 220 million years. The Cephalocarida (Sanders 1963; Hessler and Newman 1975; Hessler 1992; Schram 1986; Wills 1998) are all small, elongate, benthic detritivores. Extant species reach lengths of between 2.0 and 3.7 mm. The fossil *Lepidocaris rhyniensis* from the Middle Devonian Rhynie Chert (Scourfield 1926) is almost certainly a cephalocarid (but see Walossek 1993), and is the only fossil representative of the group. Hence, a gap of 399 million years is implied within the Cephalocarida alone.

The Anostraca (Calman 1909; Fryer 1992) can reach lengths of 100 mm. Most filter detritus or micro-organisms from the water column, but a few are active predators. The cuticle of extant species is thin, and the fossil record equivocal. Putative anostracans are reported from the Carboniferous (Tasch 1969) and the Devonian (Schram 1986), but the earliest fossil that can be assigned to the group with any confidence is Miocene in age (Palmer 1957). Most workers consider the Anostraca to form a clade (Branchiopoda) with the Notostraca, Kazacharthra, Conchostraca and Cladocera, also implying large ghost ranges. The extant Remipedia (Yager 1981; Schram 1983; Schram and Emerson 1986) have as many as 32 podous trunk somites, and reach a length of 30 mm. The Lower Pennsylvanian *Tesnusocaris goldlichi* is the only fossil ascribed to the group.

Copepods are among the most abundant crustacean taxa, with perhaps 10,000 living species in 177 families. Unfortunately, fossils are virtually non-existent. Of the eight modern orders, only three contain even tentatively assigned fossils. A harpacticoid (*Cletocamptus*) and an unnamed cyclopoid have been reported from the Middle Miocene of the Mojave Desert (Palmer 1960), while a parasitic siphonostomatoid (*Kabatarina pattersoni*) was recorded from the gills of a fish from the Mid-Cretaceous Santana formation of Brazil (Cressy and Patterson 1973). No published phylogenies resolve these three orders as the most plesiomorphic (parasitic siphonostomatoids are highly derived), and therefore imply the existence of numerous ghost ranges (e.g. Boxshall 1986; Ho 1994; Huys and Boxshall 1991).

Cladograms of the Eumalacostraca are extremely incongruent with the fossil record (Wills 1998), Table 1. The most recent tree of the whole group derived from a parsimony analysis of morphological characters (Wills 1998) yielded an RCI of 8.08, an SCI of 0.41 and a GER of 0.06. Another (Schram 1986) had a lower RCI (1.73) and SCI (0.27), but a slightly higher GER (0.13). The 'traditional' model (illustrated by Schram 1981) had a much better RCI (28.60) and SCI (0.42) but an equally poor GER (0.12). Trees for the peracarids alone also scored dismally: RCI = 55.49, SCI = 0.40, GER = 0.03 (Fryer 1965): RCI = 34.74, SCI = 0.50, GER = 0.02 (Pires 1987); RCI = 53.13, SCI = 0.40, GER = 0.09 (Watling 1981).

Wagner and Sidor (2000) have demonstrated that the theoretical minimum SCI (with an infinitesimally poor record) is 0.50. Values significantly lower than this (as in many of the above cases) suggest one of two things (P.J. Wagner, personal communication 2000). (1) There is a driven trend (*sensu* McShea 1994) toward an increase in preservation potential. This will result in more derived (later) taxa being more likely to leave fossils than less derived taxa. In extreme cases, the derived (and more fossilizable) forms may appear in the record before their older, more basal and less skeletonized relatives. (2) There are driven trends in other morphologic features. This may result in the derived members of sister clades independently acquiring a sufficient number of superficially homologous characters for parsimony to mistakenly consider those features to be primitive. This will reverse the branching order of the cladogram.

It should be noted that heavy sclerotization and mineralization appears to have evolved on several occasions within the arthropods as a whole (trilobites, ostracods, cirripedes, several groups of eumalacostracans). Arthropods with the most fossilizable skeletons often have much more weakly skeletonized but otherwise morphologically rather similar sister taxa. The most heavily mineralized eumalacostracans are among the decapods and stomatopods. No cladograms resolve these as sister groups, and all consider the decapods to be highly derived. Only massive homoplasy among the Crustacea as a whole could invalidate this conclusion. A driven trend towards increased preservation potential within the Eumalacostraca is therefore a possibility.

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Table 1. Various measures of stratigraphic congruence for a small sample of cladograms of eumalacostracans, chelicerates and hexapods

Author	Group	GER*	GER percentage 'significance'†	Percentage of random trees with better GER then observed‡	Percentage of random trees with better GER 'significance' than observed §	SCI*	SCI percentage 'significance'†	Percentage of random trees with better SCI than observed‡	Percentage of random trees with better SCI 'significance' than observed§
Schram (1986)	Eumalacostraca	0.128	79.2	88.2	80.1	0.273	100.0	84.0	95.2
Wills (1998)	Eumalacostraca	0.060	99.0	99.5	98.0	0.410	100.0	99.1	95.5
Weygoldt & Paulus (1979)	Chelicerata	0.702	1.6	2.8	1.4	0.600	3.8	10.4	4.6
Hammen (1989)	Chelicerata	0.558	12.1	13.3	13.9	0.500	56.0	95.5	39.5
Shultz (1990)	Chelicerata	0.459	33.0	21.8	31.4	0.667	7.0	3.4	4.2
Selden & Dunlop (1998)	Chelicerata	0.646	1.0	0.0	1.4	0.631	1.0	2.8	1.2
Ross (1965)	Hexapoda	0.274	74.2	89.5	75.1	0.296	99.8	97.4	95.2
Kristensen (1975)	Hexapoda	0.296	92.0	63.8	89.3	0.385	99.2	86.5	94.4
Daly *et al.* (1978)	Hexapoda	0.544	5.5	2.8	5.5	0.500	17.5	19.0	13.4

*Raw value.
†Percentage of randomized range reassignments yielding a value equal to or better than that for the original data.
‡Percentage of randomized trees with a raw value equal to or better than that for the original data.
§Percentage of randomized trees with a significance equal to or better than that for the original data.

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All cladograms resolve eumalacostracans with homonomous appendages and weak tagmatization (e.g. syncarids) towards the base of the clade. These forms are phenetically most similar to non-eumalacostracans (entomostracans). A trend towards specialization of appendages and increased tagmosis in arthropods is almost certain (Hessler and Newman 1975; Schram 1982; Wills *et al.* 1998), and it is difficult to see what the selective pressures for reintegration and secondary homonomy of limbs might be. Although unlikely, such a shift might be mediated by heterochrony in several parallel lineages, and this homoplasy might then be sufficient to mislead parsimony into reversing the branching order in sections of the tree. On balance, it seems more probable that trends for increased limb specialization and preservation potential both run in the same direction, and that the latter results in the negative correlation between branching and preservation order.

Randomization tests based on 1000 reassignments of the eumalacostracan range data over the same tree topologies indicated no trees were significantly more congruent than random. In some cases, congruence was actually significantly worse than random, with 99% of the permuted GER values for the tree of Wills (1998) being equal to or better than those for the original data. Of 1000 random *trees*, only 15 were *less* congruent with stratigraphy (as measured by the GER) than the observed tree of Wills (1998). When these random trees were themselves subjected to randomization tests, only 20 (2%) gave values as bad as or worse than the original. GER congruence is therefore worse than for purely random trees with $P < 0.01$. Schram's (1986) tree for the Eumalacostraca performed almost as badly (Table 1). These results suggest one of three possibilities: (1) homoplasy (especially driven trends) has flipped major portions of the tree, making early primitive members *appear* derived within their respective subclades, and with independently but similarly derived members being considered primitive; (2) the phylogeny borders on random; (3) preservation rates are nearly inifinitesimal. The first possibility has been considered above, and is thought unlikely. The second possibility implies that several independent workers have selected sets of characters that all suggest entirely misleading patterns of relationships. Moreover, these cladograms share much in common with many traditional trees, as well as most of those derived from molecular data (which also have stratigraphic congruence worse than most random trees). In summary, only rampant homoplasy in morphological characters and a wholly misleading set of molecular signals could result in trees that are genuinely less accurate than most random trees. The last possibility (that preservation rates are infinitesimal) is perhaps the most likely.

Apart from taxa restricted exclusively to the Recent, many eumalacostracan and hoplocarid orders have their first fossil representatives in a relatively short interval from the Late Devonian to the Early Carboniferous. Most eumalacostracan bodyplans therefore appear to have been deployed in a rapid radiation (Schram 1981; Wills 1998). It is unlikely that the group would acquiesce for some 350 million years before radiating again in several parallel lineages near the Recent. Hence, it seems probable that several apparently solely Recent groups really have an ancient history. Other lines of evidence support this. For example, in the Thermosbaenacea (Schram 1986), trans-Atlantic links of closely related modern taxa (Stock 1976; Stock and Langley 1981) strongly suggest the breakup of an ancient group with a Tethyan biogeography (Maguire 1965). Many groups are also reported from just one or two fossil occurrences. The chances of these isolated finds genuinely coinciding with the origins of groups are slight.

3.3. Gaps between the major groups of Chelicerata

The palpigrades have the least extensive fossil record of any chelicerate order. Unequivocal fossils are known only from the Late Tertiary (Rowland and Sissom 1980). The putative palpigrade, *Sternarthron zitelli*, from the Jurassic Solnhofen Limestone of Germany was synonymized with the insect *Propygolampis* by Carpenter (1992). Palpigrades are relatively small arthropods, reaching 3 mm in length at most. Many features of their morphology (such as a divided carapace) suggest a primitive status within the arachnids (Savory 1971; Weygoldt and Paulus 1979; Shultz 1990), but these may be secondary adaptations to small size rather than plesiomorphies. Almost all placements imply that the greater part of palpigrade history is not recorded. Shultz (1990) resolved palpigrades as the sister group of a clade comprising the Araneae, Amblypygi, Uropygi and Schizomida. The Uropygi and Amblypygi have records that extend back as far as the mid-Carboniferous, but the earliest spider (*Attercopus* from the Gilboa Formation of New York; Shear *et al.* 1987) is Pragian (Lower Devonian) in age, suggesting a ghost

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range for palpigrades in the order of 394 million years (or 247 million years if *Sternarthron* is a palpigrade). Hammen (1989) resolved palpigrades as the sister group of the mite clade Actinotrichida (which he split from the other mites, the Anactinotrichida), implying a ghost range back to the early Devonian. A similar palpigrade ghost range is implied by the phylogeny of Weygoldt and Paulus (1979), who resolved palpigrades as the sister group of a clade containing Pseudoscorpiones, Solifugae, Ricinulei, Acari and Opiliones, of which the Acari (Actinotrichida + Anactinotrichida) are the oldest group.

Many authors (e.g. Weygoldt and Paulus 1979; Lindquist 1984; Shultz 1990) unite the Actinotrichida and Anactinotrichida within the clade of Acari (mites). The former group contains larger individuals, and has a record extending back to the Lower Devonian. The Anactinotrichida are recorded throughout most of the Tertiary, but a ghost range of 343 million years is implied. The probable sister group of the mites, the Ricinulei, are blind chelicerates, reaching lengths up to 20 mm. Their earliest record is mid-Carboniferous, implying another ghost range of 74 million years. Some workers (e.g. Weygoldt and Paulus 1979) resolve the Opiliones (including the familiar 'harvestmen') as the sister group of all the above taxa. From the earliest opilionid (= Early Carboniferous) to the earliest mite is a gap of 47 million years. Other workers place the Opiliones as sister to the Scorpions, Pseudoscorpions and Solifugae (e.g. Shultz 1990; Selden and Dunlop 1998) (a gap of 89 million years), or possibly the Xiphosura and Scorpiones (Hammen 1989) (ghost range of 186 million years).

The Schizomida are either regarded as the sister group of the Uropygi (whip scorpions), or as a clade within them (opposing another uropygid clade, the Thelyphonida). Like the palpigrades, schizomids have several features associated with miniaturization, including a divided carapace. The Thelyphonida have a record extending back to the mid-Carboniferous, while the first record of schizomids is Chattian (middle Tertiary).

Of the four published cladograms of all chelicerates tested in Table 1, the tree of Selden and Dunlop (1998) was by far the most congruent, and the only tree with significant deviation from random. Despite appreciable ghost ranges, trees of chelicerates are far more congruent with stratigraphy than trees of the Eumalacostraca (Table 1).

3.4. Gaps between the major groups of Hexapoda (Insecta)

Most workers (e.g. Hennig 1969; Kristensen 1975; Boudreaux 1979; Kukalová-Peck 1987, 1991; Štys and Bilinski 1990) regard the Protura and Collembola (springtails) as sister groups. Modern collembolans reach lengths of about 6 mm, and are represented by about 2000 species, while modern proturans are somewhat smaller, much rarer insects and represented by about 100 species. While the Collembola have a fossil record dating back almost 400 million years (with numerous intermediate occurrences from Baltic amber; Ross and Jarzembowski 1993), no fossil proturans have been reported.

Fleas (Siphonaptera) are usually either regarded as the sister group of true flies (Diptera; e.g. Daly *et al.* 1978) or scorpion flies (Mecoptera; Ross 1965; Kristensen 1975). Fleas are first reported from the base of the Cretaceous, while the first true flies occur as long ago as the Ufimian (Permian), a gap of 112 million years. Scorpion flies have an even older record, with numerous occurrences extending back to the base of the Permian.

The sister group of the Coleoptera (beetles) is almost certainly the Strepsiptera (Brusca and Brusca 1990; but see Whiting *et al.* 1997). The fossil record of beetles is very extensive with 126 families being reported (Ross and Jarzembowski 1993). The earliest beetles belong to the extinct families Oborocoleidae, Permocupedidae, Rhombocoleidae, Taldycupedidae and Tshekardocoleidae, all dating from the base of the Permian. However, the oldest strepsiperan (*Stichotrema eocaenicum*) is from brown coal deposits in the lowest Eocene of Germany (Kathirithamby, 1989). A gap of 236 million years is implied.

It is usually considered that the Phthiraptera (the sucking lice) constitute the sister group of the Psocoptera (the booklice and barklice; Ross 1965; Kristensen 1975; Daly *et al.* 1978). The fossil record of the Psocoptera comprises 30 families, and the earliest representatives (Archipsyllidae) date from the base of the Permian. The only fossils of phthirapterans are eggs of an undetermined family preserved in Baltic amber (Late Eocene; Boucot 1990). A ghost range of 253 million years is implied.

Stratigraphic congruence for three published hexapod phylogenies is given in Table 1. The tree of Daly *et al.* (1978) was significantly more congruent than random trees ($P < 0.050$), but not significantly more congruent than

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for random range assignments on the same topology. Congruence for hexapods is generally better than in the Eumalacostraca, but not as good as the Chelicerata.

4. RESULTS

Results for 1000 trees of arthropods and other taxa are summarized below. Randomized range reassignment over a static topology represents the simplest measure of congruence controlling for most sources of bias. Results from these tests are presented alongside raw GER and SCI values.

4.1. Gap excess ratios

The GER distributions for all taxa, tetrapods and fish (Figure 1a–c) are all skewed towards higher (= 'better') values (−0.465,−0.787 and −0.182 respectively). The distribution for arthropods (Figure 1d), by contrast, is skewed towards lower values (0.245). There are relatively large numbers of trees with GER values between zero and 0.050 (13% for all taxa), and therefore whose congruence is about as low as it can be. Kolmogorov-Smirnov tests demonstrate significant differences ($P < 0.050$) between all possible pairs of distributions in Figure 1.

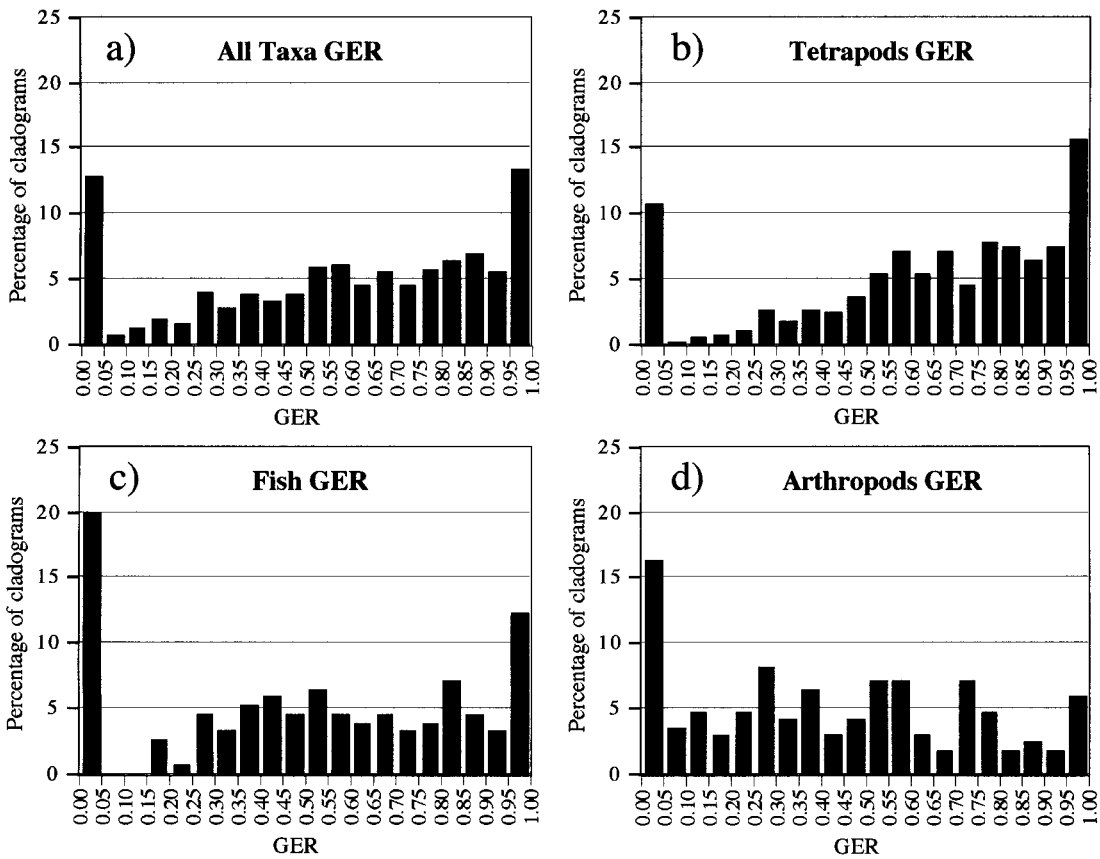

Figure 1. Frequency distributions of GER values for various taxonomic partitions of the data set. (**a**) All cladograms together; (**b**) tetrapod cladograms; (**c**) fish cladograms; (**d**) arthropod cladograms.

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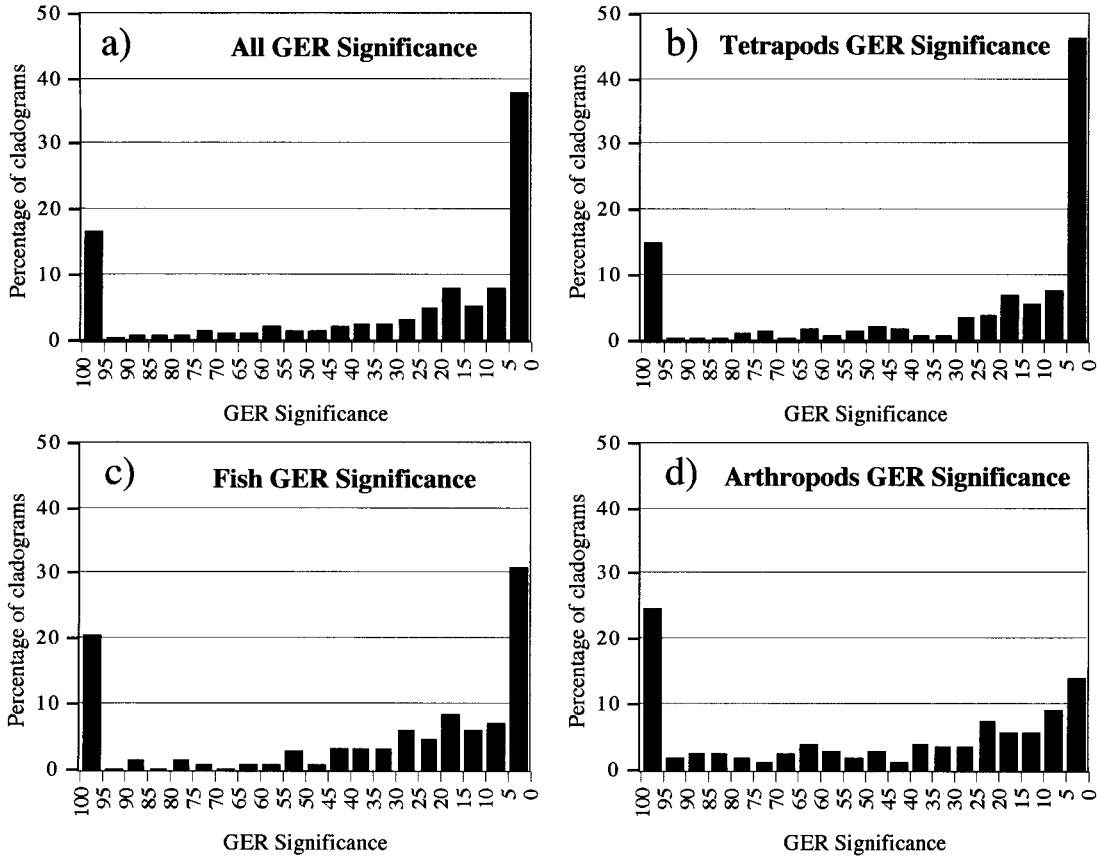

Figure 2. Frequency distribution of approximate GER significance values for various taxonomic partitions of the data set. Approximate significance is given by the percentage of randomized range reassignments that yield a GER value equal to or greater than the original data. (**a**) All cladograms together; (**b**) tetrapod cladograms; (**c**) fish cladograms; (**d**) arthropod cladograms.

However, with $P < 0.010$, distributions for fish and all taxa ($P = 0.041$), and for fish and arthropods ($P = 0.020$) are not significantly different. Congruence (measured by the GER) for arthropods (mean = 0.420) is poorer than that for tetrapods (0.637), all taxa taken together (0.580), and fish (0.512).

GER 'significances' (controlling for differences in tree size and balance) indicate a slightly different pattern of results. Although the deviation from random does not provide a statistical 'test' of congruence as such (the anticipation of perfect fit is an unrealistic biological expectation in most cases; Wills 1999), 38% of all trees have a GER value bettered or equalled by no more than 5% of randomized range reassignments. This figure is 46% for tetrapods, 31% for fish, but just 14% for arthropods. Similarly, while 16% and 15% of all trees and tetrapod trees respectively are bettered or equalled by 95% or more of randomized trees ('significantly worse' than random), this rises to 20% for fish and 25% for arthropods. Kolmogorov-Smirnov tests indicate that distributions of GER significances cannot be distinguished with $P < 0.050$ for fish (Figure 2c) and tetrapods (Figure 2b) ($P = 0.115$), and for fish and all taxa (Figure 2a) ($P = 0.067$). All other pairwise comparisons indicate significant differences between distributions with $P < 0.010$. Hence, the distribution of GER significances for arthropods (Figure 2d) differs from that of all other groups, and has a much lower mean.

It has also been informative to partition data for all cladograms according to broad habitat type (marine, terrestrial and both) (Figure 3). While 30% of cladograms for terrestrial groups were 'significantly better' than random using the GER (equalled or bettered by 5% or less of random values), this figure was 41% for marine groups, and

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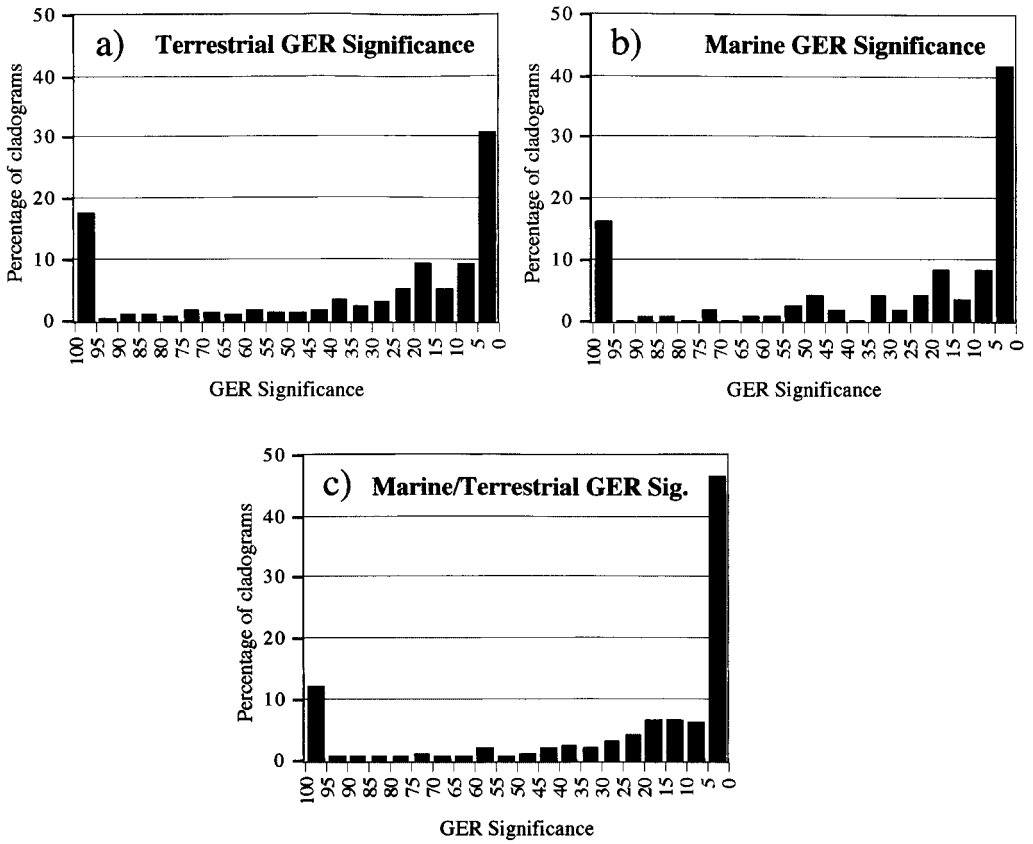

Figure 3. Frequency distribution of approximate GER significance values for division of the data set into broad habitat type. (**a**) Cladograms of terrestrial taxa; (**b**) cladograms of marine taxa; (**c**) cladograms of terrestrial and marine taxa, and/or amphibious taxa.

47% for groups inhabiting both environments. Intuitively, we would expect a better fossil record for marine taxa than their terrestrial counterparts, but this has not been demonstrated on the basis of RCI or SCI values for a smaller sample of cladograms (Benton and Simms 1995). While the overall distributions of GER significance for marine and terrestrial trees do not differ significantly at $P < 0.050$ (Kolmogorov-Smirnov test, $P = 0.598$), cladograms for groups reported from both habitats have a significantly 'better' distribution than those restricted to either terrestrial or marine environments ($P < 0.010$).

4.2. Stratigraphic consistency index

SCI values are heavily influenced by factors such as tree balance, tree size, and the distribution of range values. Certain values arise more commonly than others for reasons more connected with tree topology than congruence *per se*. Assuming there are no identical origin dates, topology (or more precisely, tree balance) sets bounds on the SCI. Perfectly balanced trees (those in which every node supports the same number of terminals as its sister node) of taxa with different origination dates will always have a SCI of 0.50. For each pair of nodes, if one is congruent, the other must be incongruent (and *vice versa*). Entirely pectinate trees of taxa with different origin dates can have values between 0.00 and 1.00. Hence, even the distribution SCI values for all 1000 trees is irregular. A total of 138 trees have a SCI of exactly one-half, 75 trees exactly one-third, and 38 exactly one-quarter, while only a handful of trees have values immediately either side of these simple fractions. The overall distribution (Figure 4a) is therefore

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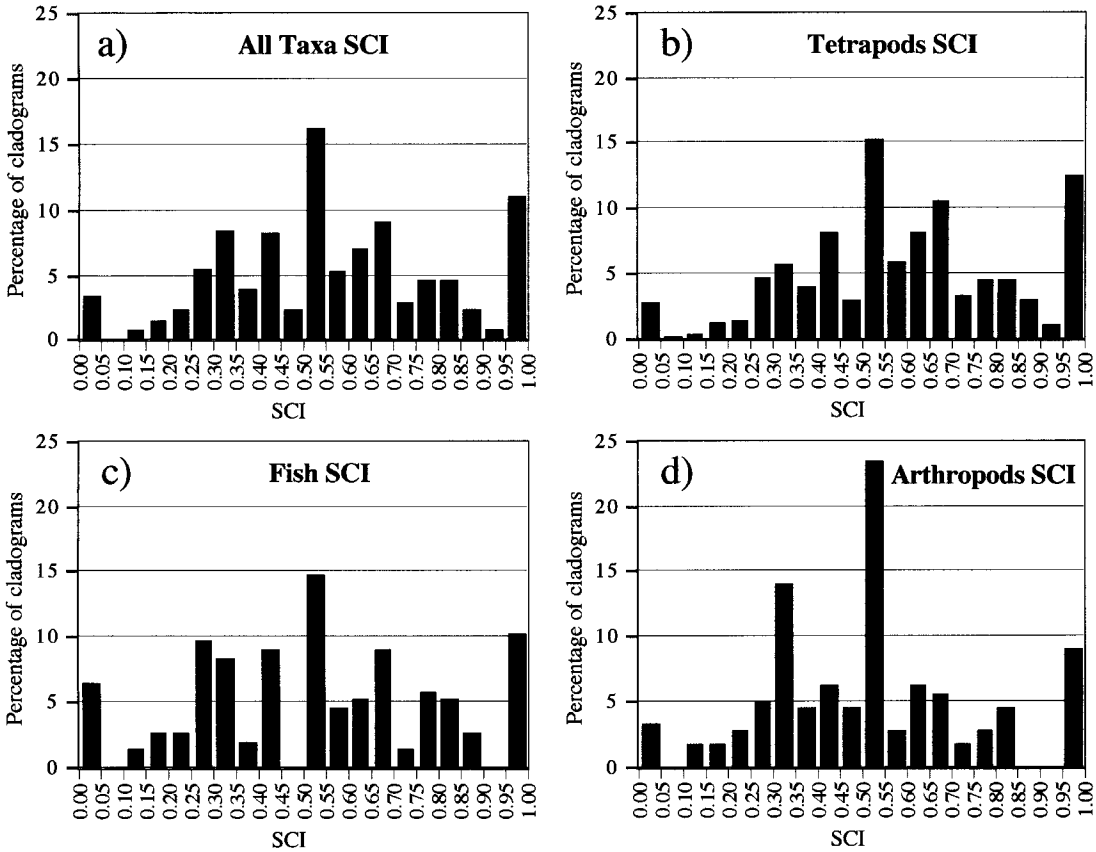

Figure 4. Frequency distributions of SCI values for various taxonomic partitions of the data set. (**a**) All cladograms together; (**b**) tetrapod cladograms; (**c**) fish cladograms; (**d**) arthropod cladograms.

rather jagged. The distribution for tetrapods (Figure 4b) is similar to that for all taxa together (means of 0.584 and 0.555 respectively), and the two cannot be distinguished statistically (Komolgorov-Smirnov test, $P = 0.145$). The distribution for fish contains slightly more lower values (mean 0.518), but is still indistinguishable ($P = 0.230$) from that for all taxa. Distributions for fish (Figure 4c) and tetrapods can be distinguished with $P < 0.050$ ($P = 0.013$), and all other pairwise comparisons indicate differences with $P < 0.010$. The difference between arthropods (Figure 4d) and tetrapods ($P = 0.001$) is the most marked, and the group has the lowest mean (0.501).

SCI significance shows a much less ragged distribution (Figure 5a), and can be compared with the distribution for GER significance (Figure 3a). SCI significances for groups were lower, on average, than the corresponding GER significances. Over all 1000 trees, 822 had a higher GER significance than SCI significance. While some 38% of trees had a GER equalled or bettered by no more than 5% of randomized range reassignments, this figure was just 18% for the SCI. The SCI randomization 'test' is far more difficult to pass than the GER test, because there are fewer possible SCI values than GER values for any given tree, and similar SCI values are more readily converged upon as a function of topology than GER values. Despite these strictures, there are significant differences ($P < 0.050$) between the SCI significance distribution for arthropods (Figure 5d) and all other groups ($P = 0.020$ for the comparison with fish (Figure 5c), $P = 0.001$ for tetrapods (Figure 5b) and $P = 0.001$ for all taxa (Figure 5a)). While as many as 20% of tetrapod and 23% of fish cladograms passed the SCI randomization 'test' with $P < 0.050$, this figure was just 7% for arthropods. Similarly, 30% of arthropod cladograms had a 'significantly worse' SCI than random, compared with 25% for fish and just 15% for tetrapods.

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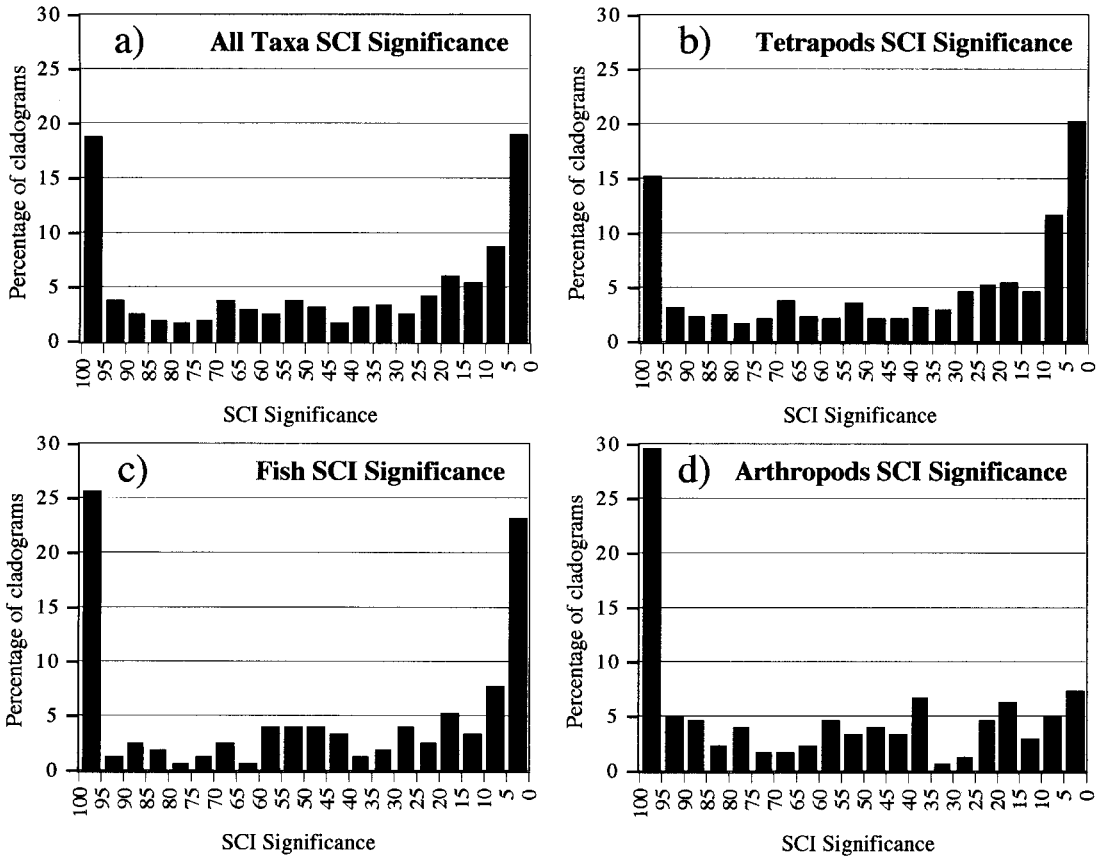

Figure 5. Frequency distribution of approximate SCI significance values for various taxonomic partitions of the data set. Approximate significance is given by the percentage of randomized range reassignments that yield a GER value equal to or greater than the original data. (**a**) All cladograms together; (**b**) tetrapod cladograms; (**c**) fish cladograms; (**d**) arthropod cladograms.

4.3. Differences in congruence through time

It has also been informative to partition trees temporally into those with fossil records predominantly in the Palaeozoic and those predominantly in the post-Palaeozoic (Figure 6). Comparisons of overall distributions of congruence for all Palaeozoic and post-Palaeozoic cladograms indicate no significant differences for either GER significance (Figure 6a) ($P = 0.255$) or SCI significance (not shown) ($P = 0.972$). At the broadest scale, therefore, congruence for Palaeozoic trees is not significantly different from that for post-Palaeozoic trees. However, Palaeozoic/post-Palaeozoic comparisons for tetrapods, fish and arthropods yielded P values for GER significance of 0.039, 0.014 and 0.015 respectively, and for SCI significance of 0.008, 0.155 and 0.001 (all significantly different with $P < 0.050$, except for the fish SCI significance). At the extreme of the distribution for arthropods, while 24.6% of Palaeozoic cladograms are equalled or bettered by no more than 5% of randomized runs, the corresponding figure for post-Palaeozoic trees is just 7.9%.

In an attempt to increase temporal resolution, the data set was divided into five bins: (1) trees with origins entirely in the Palaeozoic; (2) trees with origins spanning the Palaeozoic and Mesozoic; (3) trees originating entirely in the Mesozoic; (4) trees with origins spanning the Mesozoic and Cenozoic; and (5) trees solely located in the Cenozoic (see Benton *et al.* 2000). Both the GER and SCI are biased by the range of origination dates, and trees spanning two eras potentially have longer ranges than those restricted to just one. The use of significances rather than raw values controls for some of this bias. There are insufficient trees in some bins to plot frequency

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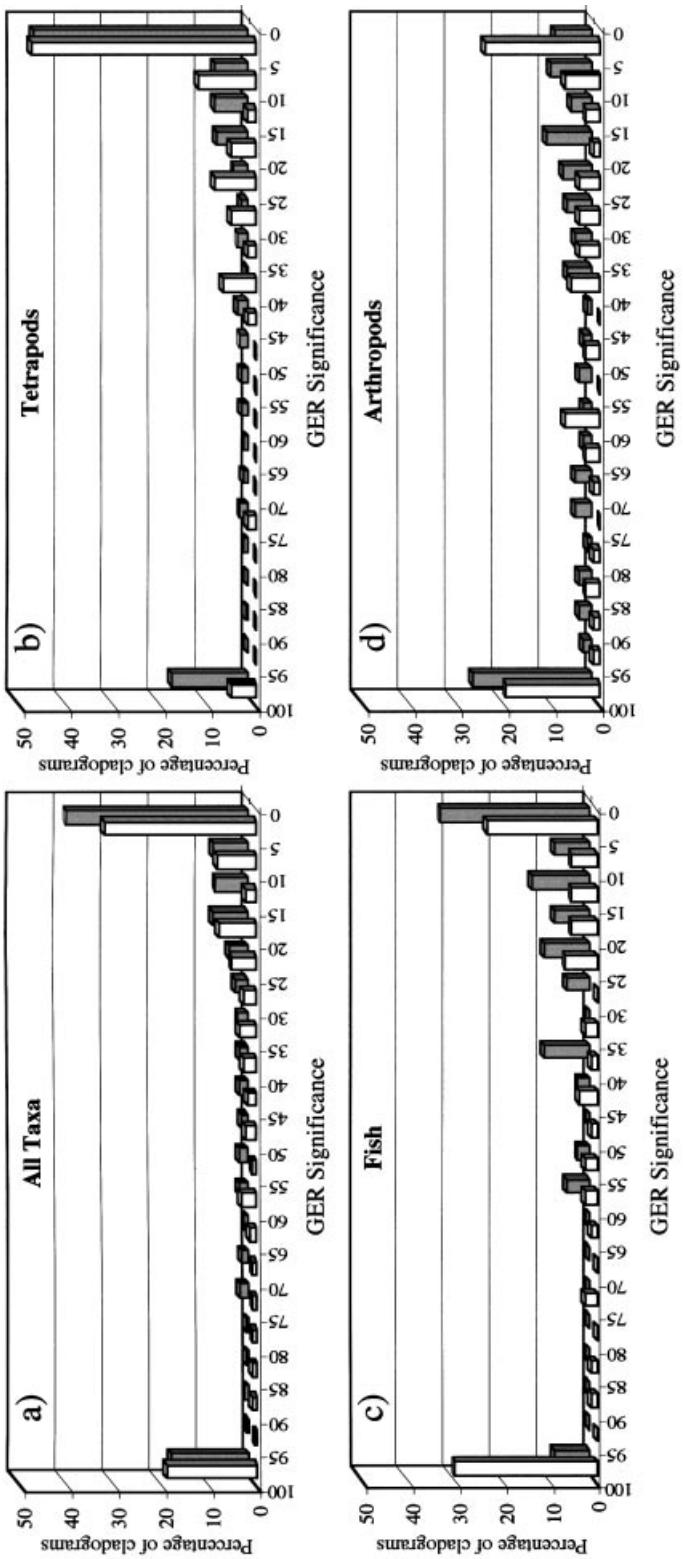

Figure 6. Frequency distribution of approximate GER significance values for various taxonomic and stratigraphic partitions of the data set. White bars (front row) represent Palaeozoic and mostly Palaeozoic cladograms. Grey bars (back row) represent post-Palaeozoic and mostly post-Palaeozoic cladograms. (**a**) All cladograms together; (**b**) tetrapod cladograms; (**c**) fish cladograms; (**d**) arthropod cladograms.

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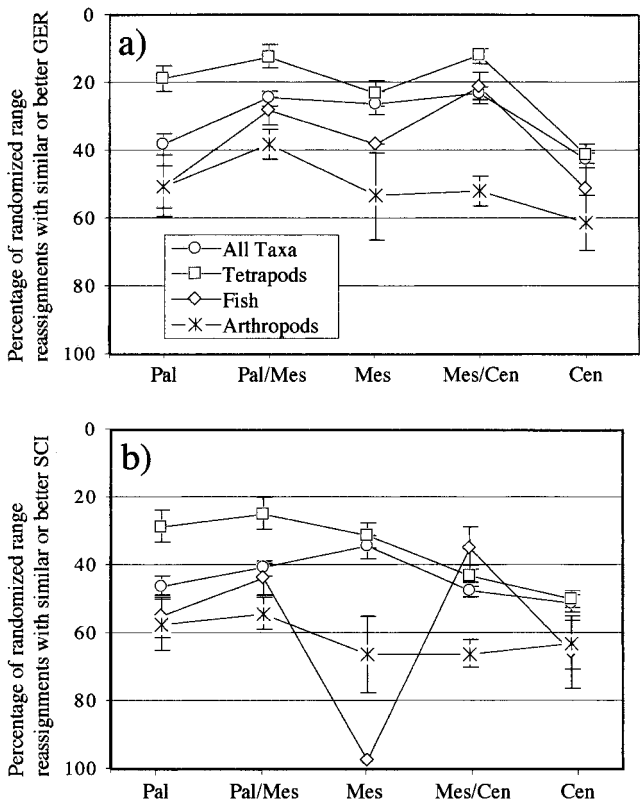

Figure 7. Mean congruence values for taxonomic and stratigraphic divisions of the data set ($\pm$ 1 standard error). Stratigraphic divisions: Pal, cladograms with origins entirely within the Palaeozoic; Pal/Mes, cladograms with origins spanning the Palaeozoic and Mesozoic; Mes, cladograms with origins entirely within the Mesozoic; Mes/Cen, cladograms with origins spanning the Mesozoic and Cenozoic; Cen, cladograms with origins entirely within the Mesozoic. (**a**) Approximate GER significance; (**b**) approximate SCI significance.

distributions for all four groups. Instead, mean GER and SCI significances are illustrated (Figure 7). There is no systematic decrease in congruence with increasing antiquity of the bin, whether for all taxa taken together, or for subgroups. For most temporal divisions, mean GER significance decreases in the order: tetrapods, all taxa, fish, arthropods. All of the time bins for both GER and SCI significance show significant difference ($P < 0.050$) between arthropods and tetrapods, and arthropods and all taxa. Again, the fossil record of arthropods is significantly less congruent with cladograms than a broad sample of other taxa.

In addition, the tetrapod GER 'significance' values for solely Palaeozoic tetrapod trees are themselves significantly better than those for solely Cenozoic tetrapods. The SCI 'significance' values for the tetrapod record indicate a significant difference in mean congruence for any of divisions 1, 2 and 3 versus either 4 or 5 ($P < 0.050$). If anything, therefore, aspects of congruence for at least one group appear to significantly *improve* with age.

5. DISCUSSION

On several measures, cladograms of arthropods show lower congruence with the fossil record than a large sample of cladograms of various other taxa. Arthropod trees are dramatically less congruent than tetrapod cladograms, either considered as a whole or when divided into broad temporal bins.

There are a variety of possible reasons for the relatively poor matching of phyletic branching order and the sequence of fossil appearance of the Arthropoda. First, it is possible that arthropod cladograms are less accurate

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or 'true' than those of tetrapods or other clades. While the relationships of many arthropod groups are highly contentious, this is also true of many other large taxa. A tree with a low overall consistency index (CI) need not be inaccurate, and in reality might faithfully reconstruct the character transitions that have taken place in the evolution of a group. Even arthropod trees with notoriously low CIs (e.g. see Gould 1991, 1993; Briggs *et al.* 1992; Wills *et al.* 1994) are within the range of values observed for other data sets of a comparable size (Archie 1989a; Archie and Felsenstein 1993; Ridley 1993). The resolution of numerous most parsimonious trees for a single data set, or the existence of numerous competing phylogenies for a particular group need not imply that most (or indeed any) will necessarily be particularly incongruent with the fossil record. Controversy rages over the relationships of amniote groups (e.g. Hedges and Maxon 1996) and mammal orders (see Shoshani and McKenna 1998), but congruence is reasonable or good for most cladograms of these taxa. Clearly, the accuracy of a given cladogram can never be tested against reality, and most tests of 'confidence' provide measures of the internal consistency of the data (e.g. bootstrapping (Felsenstein 1985), permutation tail probability (PTP) (Faith and Cranston 1991), Homoplasy excess ratio (HER) (Archie 1989b)).

Wagner (2000b) showed that rates of homoplasy in trilobites significantly exceeded those in vertebrates, echinoderms or molluscs, and predicted that cladograms of trilobites should be less accurate than cladograms of these other groups. However, trilobites represent only a small fraction (4%) of the total arthropod data set considered here. Whether homoplasy is similarly widespread in other arthropod groups has yet to be tested directly. Arthropods as a whole preserve a large number of characters particularly amenable to discrete coding and phylogenetic analysis (Briggs and Fortey 1989). However, evidence suggests that many markedly similar structures (e.g. eyes and mandibles) have arisen on numerous occasions in response to similar selection pressures (Wills *et al.* 1994). It might also be considered that while topologically very similar cladograms for a given group might all be very accurate, in a group of topologically very dissimilar trees at least some relationships will be incorrect. Topological variability for arthropod trees appears comparable to that in tetrapods, and that in the rest of the data set. Variability for arthropods is greatest for the deeper (older) sister groupings, and curiously these appear to be slightly more congruent with stratigraphy on average than the higher, less contested relationships.

It is also possible that some taxa treated as terminals in the sample of published studies are actually paraphyletic. This implies that some groups arise out of others (e.g. tetrapods out of fish), and that ghost ranges are overestimates or wholly unnecessary. This issue has been discussed elsewhere (Shultz 1994; Selden and Dunlop 1998; Wills 1999; Wagner 2000a). However, a species cladogram is consistent with a number of species trees, where the latter may include information on ancestry (see Wagner (1995, 2000a) and references therein). Where terminals are higher taxa, all groups are assumed to be monophyletic, and if this is true then the construction of ghost ranges is legitimate. However, if this is untrue, then although some or all of the ghost ranges are unnecessary, the 'correct' cladogram will be the same. Assume that the observed ranges represent the actual extent of the groups under consideration (some of which are paraphyletic). The erroneous imposition of ghost ranges onto these groups will nevertheless yield the minimum possible MIG (G_{min}) for the correct cladogram, and accordingly result in a GER of 1.00 (maximum congruence). As observed ranges become a smaller fraction of the true ranges, the potential arises for an incorrect cladogram to have the smallest MIG. However, this occurs for cladograms of monophyletic terminals as well as paraphyletic groups. Hence, even if $n-1$ terminals are paraphyletic, the GER still provides a legitimate test of congruence between the order of fossils and the order of branching.

Shultz (1994) argued that many ghost ranges probably result from a failure to correctly assign fossils to their respective groups. Rather than sister groups diverging in a geological instant so as to yield lineages with all of their diagnostic features in place, these defining characters might only be acquired in sequence over an extended period. The earliest members of a group might therefore not be recognized as such, and possibly be assigned to the sister group (if phenetically more similar to them). Shultz (1994) also contended that divergence between sister lineages might occur with no consequent differences in morphology, behaviour or genetics. Selden and Dunlop (1998) argued that this position is unsustainable, and that at least one apomorphy must support each clade. This suggests that the correct assignment of fossils will often be possible with greater systematic rigour, thereby avoiding spuriously long ghost ranges.

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Wagner and Sidor (2000) performed a series of simulations to investigate the relationship between age rank/clade rank (ARCR) congruence indices (such as the SCI) and sampling intensity (record completeness). They revealed that this relationship was good for stem-based monophyletic groups (those defined at or near branching points rather than at the interval where all diagnostic features of the crown were acquired). They also found a good relationship where investigators included taxa without any *a priori* assumptions concerning monophyly or polyphyly. However, where all taxa were constrained to be apomorphy-based monophyletic groups, the relationship between congruence and sampling was a poor one. Wagner (2001) repeated these simulations for ghost-range ('stratigraphic debt') based indices of congruence (such as the GER). The deliberate *exclusion* of paraphyla created artificial gaps in sampling, and exaggerated the apparent extent of ghost ranges. Wagner (2001) discovered that stem-based monophyla inflated the extent of gaps most at high sampling intensity, whereas apomorphy-based monophyla exaggerated most at low sampling rates. These results are unsurprising, since cladograms represent hypotheses of the order in which lineages diverged (applying to stem-based monophyletic taxa) and the order in which morphologic grades appeared (which applies to paraphyletic taxa relative to derived monophyletic groups).

A number of possible sources of bias in congruence studies were discussed by Benton *et al.* (2000), including tree size, taxonomic level of the cladograms considered, the span of origin dates and temporal resolution. These factors are similar for the various divisions of the 1000 cladogram data set discussed here, and are certainly not distributed so as to deflate the apparent mean congruence of the arthropod trees. Excessive splitting of taxa can either reduce a record to numerous short fossil ranges, or greatly increase the apparent extent of observed ranges if all the subgroups persist a long time. These effects will tend to respectively decrease and increase the RCI. Excessive splitting of closely related taxa could inflate the apparent deviation of the GER from random, particularly if all taxa appear in the record at the same or a similar time.

Wagner and Sidor (2000) discussed several other factors that will tend to inflate ARCR indices (e.g. the SCI) when the *average* rate of sampling stays constant. These include high temporal variation in sampling intensity, low extinction rates, budding rather than bifurcating patterns of speciation, cladogram inaccuracy, and (to a lesser extent) large clade size. The relationship between some of these factors and the extent of ghost ranges (stratigraphic debt and GER) is less straightforward (Wagner 2001). High temporal and intraclade variation in sampling rate decreased debt when median sampling rate was relatively low, but slightly inflated debt when sampling rate was high. At any given, *constant* sampling rate, clades with high rates of origination and extinction had significantly smaller sums of ghost ranges than clades with low rates of origination and extinction. At a low and constant sampling rate, clades in which budding cladogenesis predominated had less stratigraphic debt than clades in which bifurcating cladogenesis was the rule. At a high sampling rate, the reverse was true. The findings from these simulations suggest that where significant differences in congruence between clades exist, quantitative tests will be necessary to establish precise reasons for these differences (Wagner 2001).

The existence of ghost ranges *per se* is unsurprising, even with relatively high rates of preservation per interval (P. J. Wagner, 2000, personal communication). Suppose the preservation rates per unit of geological time (whatever these might be) are uniform for all lineages at 0.50. Assume, also, that there is no extinction. The probability of sampling both sister taxa in the interval of their origin is therefore $0.50 \times 0.50 = 0.25$ (25% of taxa). Similarly, there is a 0.25 probability that neither taxon will be sampled in the interval of origin (25% of taxa), in which case there is also a 0.25 probability that both members of a sister pair will make their fossil debuts in the interval immediately above the one in which they truly originated. Hence $25\% \times 0.25 = 6.25\%$ of sister pairs will first fossilize together 'one interval up', giving the illusion of the same first appearance. The probability of sisters appearing together for the two intervals is therefore $0.2500 + 0.0625 = 0.3125$. Integrating this out to infinity, the probability of co-origination becomes 0.3333 (one-third of all sister taxa first appear in the record together). Now suppose that there is extinction, implying that both taxa might not survive into subsequent intervals in order to be preserved. If the extinction rate is uniformly 0.5 per geological interval, then only 25% of sister pairs will survive into the next interval. Only 25% of this surviving 25% of pairs will not already have one or both members sampled in the true interval of origin (therefore 6.25% of taxa can be sampled together in the next interval up). Of these, only 25% will

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actually be sampled together (= 1.56%). This integrates out to our expecting 26.67% of sister taxa to share the same interval of first occurrence.

In fact, the assumption of constant rates of preservation between lineages and through time is certainly an oversimplification. Highly mineralized taxa are much more likely to leave fossils than lightly sclerotized forms. Taxa containing many individuals are more likely to leave a record than those containing just a few. Geographically widespread groups are more likely to be preserved than those with restricted distributions. Infaunal organisms are more likely to leave fossils than pelagic ones. These asymmetries in preservation potential between sister groups will make the existence of ghost ranges even more probable. Several examples of ghost ranges of tens or hundreds of millions of years exist for pairs of arthropod taxa whose common ancestry is uncontested in the literature. There are additional instances where all alternative published relationships nevertheless imply large gaps.

Fortey *et al.* (1995, 1997) considered that cladogenesis in lineages comprising small individuals might be an explanation for the lack of Precambrian arthropod fossils. The apparently explosive radiation in the Cambrian fossil record would therefore be the product of a parallel size increase in relatively distantly related taxa. The Cambrian may have been exceptional in providing the necessary environmental trigger for numerous lineages to respond in concert. More generally, however, the small size of individuals may have contributed to the absence of fossils for several important arthropod groups. Modern tardigrades, palpigrades, acarids, cephalocarids, mystacocarids, tantulocarids, pauropodans, proturans, diplurans, thysanopterans, most collembolans, and most cladocerans are all in the size range of 0.1–3.0 mm (many towards the smaller extreme). Although individuals in these groups may have been substantially bigger in the past, their present size almost certainly makes preservation (discovery and recognition) less likely. Also, because even the largest arthropods tend to be small relative to most tetrapods, fish, and most of the other groups in the database, comparatively large populations can exist in restricted and isolated geographical areas. Hence, discoveries of previously unknown *extant* orders and families in inaccessible or obscure settings are not uncommon. There is no reason to suppose that similar enclaves have not existed through the geological past. Even if fossils have been preserved, they may well be at least as difficult to find as their extant counterparts.

Closely related modern arthropod taxa of the same rank often contain markedly different number of species, and some groups are strikingly more abundant than others. Several orders of arthropods have only relatively recently been discovered as extant groups, let alone as fossils. The Procarididea (Eumalacostraca), for example, are represented by just a single living species (*Procaris ascensionis*), discovered in the Ascension Islands almost 30 years ago (Chace and Manning 1972), and known only from two other localities in Hawaii. The sister order to the Procarididea is the Caridea (true shrimps; Schram 1986; Wills 1998) comprising 22 families, and containing approximately 2000 living species. Recent carideans are extremely abundant, occupy a variety of habitats (pelagic, benthic, epibenthic, fresh water, brackish and marine), and are distributed throughout the world. Despite this present ubiquity, the fossil record of carideans is scant (Glaessner 1969), probably because the preservation potential of their thin cuticle is poor. While procaridids may once have been more diverse and abundant, the combination of low preservability and low numbers of individuals is a plausible explanation for the absence of procaridid fossils.

The Mictacea (Eumalacostraca) are known from just two extant species in two families: one deep-sea form (*Hirsutia bathyalis*) described from just two specimens (Sanders *et al.* 1985), the other (*Mictocaris halope*) more plentiful, and endemic to marine caves in Bermuda (Bowman and Illiffe 1985). The sister group of the Mictacea is probably a clade comprising the Amphipoda (approximately 6000 species) and Isopoda (98 families) (Schram 1986; Wills 1998). Both groups are extremely abundant and widespread today, but have patchy and disappointing fossil records (Hessler 1969; Schram 1986). Bousfield (1982) considered that there is no compelling reason to suppose that amphipod diversity was vastly lower in the past than today, nor that they had particularly restricted distributions. The absence of mictacean fossils is therefore scarcely surprising given the paucity of fossil amphipods and isopods.

The order Amphionidacea (Eumalacostraca) contains just one living species (*Amphionides reynaudii*; Williamson 1973), infrequently reported from depths of around 2000 m or more.

The absence of euphausiacians in the fossil record is particularly surprising. Modern krill range from about 4 cm to 15 cm in length, and reach densities exceeding 1000 animals/m^3 of seawater. Several authors (e.g. Dzik and

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Jazdzewski 1978; Schram 1981) have suggested candidate fossils, but none of these is particularly compelling (Schram 1986).

6. CONCLUSIONS

(1) The stratigraphic consistency index (SCI; Huelsenbeck 1994) and the gap excess ratio (GER; Wills 1999) assess different aspects of the congruence between phyletic branching order and the sequence of appearance of taxa in the fossil record (nodal consistency and the extent of ghost ranges respectively). Unfortunately, both measures are potentially biased by differences in tree size, tree balance, and the distribution of first occurrence dates for the taxa in the cladogram. Hence, the congruence of a cladogram is more appropriately measured by calculating the deviation of its SCI and GER values from the distribution of the same values when stratigraphic ranges are randomly reassigned over an identical topology (Wills 1999). This makes it possible to compare congruence for disparate trees of very different proportions. Over a sample of 1000 cladograms of tetrapods, fish, echinoderms, arthropods, other invertebrates and plants (Benton *et al.* 2000), the GER shows a weak (but statistically insignificant) correlation with its own deviation from random. The correlation between the SCI and its own deviation over the same data set is even weaker.

The deviation of GER and SCI values from random does not provide a test of statistical significance in the strictest sense. There is no reason to expect perfect congruence in most biological situations, and therefore the 'tests' are rather too difficult to 'pass'. While cladograms that are equalled or bettered by no more than 5% of the randomized data are certainly more congruent than random (and congruence can be considered 'significant'), lower levels of significance need not preclude a meaningful association.

(2) The mean SCI, GER, SCI significance and GER significance for arthropod cladograms are all significantly worse than the corresponding values for tetrapods, fish, or all taxa taken together. When split into two temporal bins (Palaeozoic and post-Palaeozoic), the same relationships hold. With five temporal divisions, some bins contain sample sizes too small for meaningful comparison. However, mean congruence values for arthropods are significantly lower than tetrapods or all taxa together for all temporal divisions of the data.

The greatest differences in the distributions of SCI, GER, SCI significance and GER significance values are those between arthropods and the other groups. Distributions for tetrapods and all taxa are the most similar, while distributions for tetrapods and arthropods are the most dissimilar. The number of arthropod trees falling in the upper 5% divisions of the GER and SCI significance are themselves significantly greater than the corresponding numbers for tetrapods or all taxa considered together. Likewise, there are significantly more arthropod cladograms in the lower 5% division of GER or SCI significances than tetrapods or all taxa together.

In general, congruence for the four taxonomic partitions of the data decreases in the order: tetrapods, all taxa, fish, arthropods.

(3) There is no indication that stratigraphic congruence is worse for cladograms of older taxa, or for trees principally spanning older portions of the record. Although previously assessed by Benton *et al.* (2000) from raw SCI, GER and RCI indices, this has also been demonstrated here for the deviations of these indices from random. This removes many effects of the potential sources of bias discussed by Benton *et al.* (2000), but these authors should be consulted for a fuller treatment.

(4) There are no significant differences in the distributions of GER significance values for partitions of the data into marine and terrestrial cladograms. Cladograms containing both terrestrial and marine taxa yielded a distribution that differed from those for either solely terrestrial or solely marine groups.

(5) There is independent evidence to suggest that levels of homoplasy among trilobites are greater than those among vertebrates, echinoderms and molluscs (Wagner 2001). Accordingly, cladograms of trilobites are anticipated to be less accurate than cladograms of these other groups. Levels of homoplasy among non-trilobite

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arthropods (96% of the present data set) have not been tested directly. However, there is no *a priori* reason to suppose that cladograms of arthropods should be less accurate than those of other taxa. Many of the biasing factors that might lower the apparent congruence of trees (see also Benton *et al.* 2000) are evenly distributed over the different splits of the data, or corrected for by the randomization procedures. At certain levels of resolution (specifically the stratigraphic level of stages and series, and the taxonomic level of families and above), there is evidence to suggest that the arthropod record is less complete than the record of tetrapods, fish, or a range of other groups considered together. However, this conclusion must be tempered. A number of other *potential* sources of bias (particularly those relating to probable cladogram quality, differences in taxonomic practice, and variations in preservation rates; Wagner and Sidor 2000; Wagner 2001) have not been directly assessed here. Moreover, conclusions cannot be generalized to all levels of stratigraphic resolution, taxa or localized environments.

(6) The fossil record of arthropods (perhaps more so than most other groups) is best characterized as one preserving many morphological intermediates, but relatively few temporal intermediates. Several important portions of the arthropod tree are sampled only by fossils (e.g. non-chelicerate arachnomorphs and marrellomorphs). In these cases, much of the information is derived from a small number of exceptional fossil sites. The information on novel character–state combinations provided by these fossils may be vital for the resolution of relationships between extant groups (Donoghue *et al.* 1989; Emerson and Schram 1998). However, these exceptional fossils may not provide the temporal resolution afforded by fossils of tetrapods.

(7) There is probably no one single reason for the apparent lower completeness of the arthropod record. Low preservation potential almost certainly plays a part. However, groups containing members with among the most resilient and mineralized cuticles (eumalacostracans and trilobites) may show among the lowest indices of congruence. For some trees, almost any random range reassignment or random tree topology yields higher congruence. This hints at a driven trend towards increased preservation potential through time in some clades. Probable sister taxa in similar environments can have hundreds of millions of years between their earliest fossil occurrences (e.g. Isopoda and Amphipoda, Euzygida and Reptantia, Mysidacea and Pygocephalomorpha). Therefore, limited exposure of suitable sediments alone is unlikely to be the explanation.

Small size is also a possible factor, with many of the longest ghost ranges being ascribed to particularly small taxa (e.g. Protura, Palpigrada and Mystacocarida). However, some minute taxa (e.g. mites and tardigrades) also have an ancient record. Fortey *et al.* (1997) noted that many large clades have particularly small taxa at their bases (e.g. tardigrades as the sister group of arthropods, and aplacophorans as basal within the molluscs). Small size may also allow the preservation of animals in taphonomic settings that would not be available to larger creatures (Seilacher 1990). In this context, it would be informative to split the data into broad size classes to test for a statistical effect.

Low diversity and, to a greater extent, low abundance of individuals are probable factors in the non-preservation of many arthropod taxa. For example, the Nectiopoda (six species), Mictacea (one species), Procarididea (one species) and Spelaeogriphacea (one species) have all been discovered within the last 50 years. Geographically restricted areas often yield hitherto unknown extant orders and families, and the same may be true for fossil groups. Palaeontological knowledge as a whole appears to be improving significantly with time (Benton and Storrs 1994). The frequency with which the rarer groups and hitherto unknown higher taxa are unearthed is still high enough to anticipate many major discoveries and significant range extensions in the future. One conclusive fossil is sufficient to set the minimum age of divergence for an entire order, class or phylum.

Many of the taxa considered prime targets for fossilization because of their environment or habitat (e.g. isopods and amphipods; Schram 1986) have some of the patchiest and least satisfactory records. It will therefore be informative to compare the extent of ghost ranges implied cladistically with the completeness of the record suggested by the frequency and distribution of fossils within *known* ranges (e.g. Fara and Benton 2000). Are the taxa reported from the smallest numbers of localities those implying the longest ghost ranges? Although these data have yet to be compiled for arthropods, it seems probable that their record would be characterized by fewer temporally 'intermediate' fossils than many other taxa (e.g. tetrapods).

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